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# HOW SPIDERS INITIATE AIRBORNE LINES

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ABSTRACT

Airborne line initiation was observed in spiders of at least 46 genera in 16 araneomorph families. At least three different methods of initiation were observed, two of which have apparently not been described previously. Two other methods of airborne line initiation described in the literature may not occur. In one araneid it was determined that the anterior spinnerets are apparently not involved in producing airborne lines.

## INTRODUCTION

It has long been known that many spiders produce airborne silk lines that are pulled from the spider by air currents and are used either as "spanning lines" that serve as bridges to distant objects (e.g. McCook 1889) or as "balloon lines" that allow the spider itself to become airborne (e.g. Bristowe 1939). It seems not to have been generally appreciated, however, that the initiation of such silk lines cannot be explained by the accepted notion that a silk line emerges from a spider's spinnerets only as a result of being pulled. Also, spiders are thought to be incapable of emitting silk lines unless the lines are drawn from their bodies by tension on silk that has already been emitted (e.g. Witt et al. 1968). Although it is reasonable to suppose that friction with moving air can pull out additional line once an airborne line has been initiated, it is not clear how production of the line is started when there is nothing on which the air can pull.

Literature accounts on this point are unclear and contradictory. Several authors have commented on the initiation of airborne lines (see Fig. 1), but few have addressed this particular problem, and some have made what are probably erroneous descriptions of the process. Bristowe (1939) stated that the spider "squeezes out a little silk" in order to start an airborne line (Fig. 1A), but as noted, this is unlikely to be true. Both Savory (1952) and Witt, Reed, and Peakall (1968) saw that spiders sometimes produce multiple lines as they descend and only hold one with a hind leg, allowing the other to blow free in the wind. Savory reported that this second line is cut at the spinnerets and flies free from an attachment above to the drag-line (Fig. 1B), and thought that the airborne line can thus only be as long as the spider's descent. As will be shown below, this description is probably incorrect. Richter (1970) stated that the lycosid *Pardosa* breaks its drag-line prior to initiating a balloon line, but did not describe initiation itself.

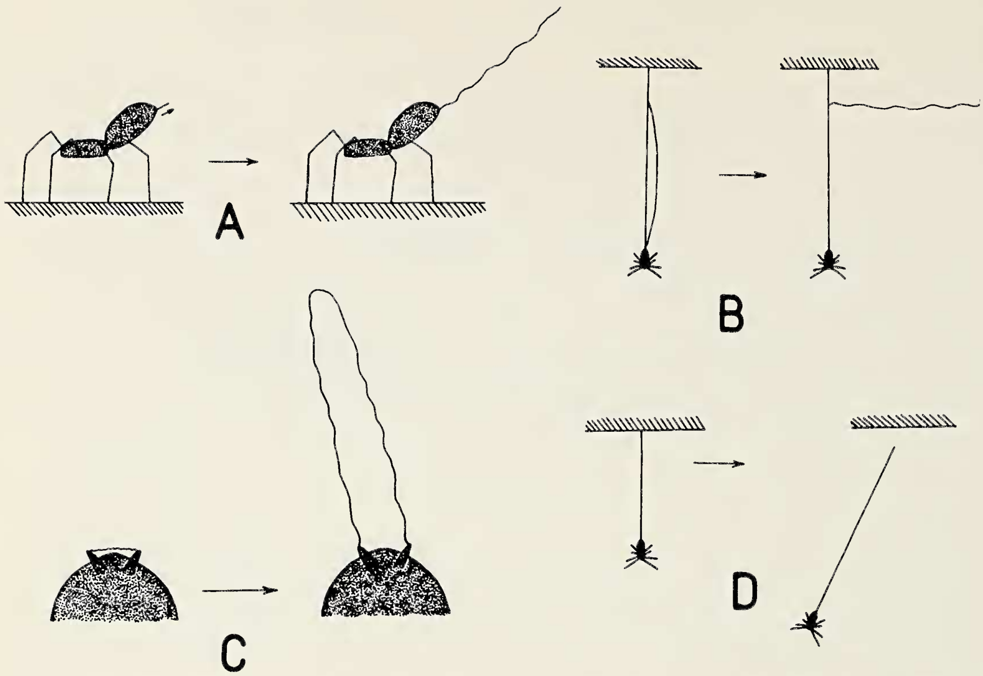


Fig. 1.—Diagramatic representation of previous descriptions of mechanisms of initiation of airborne line production. A, Bristowe (1939) thought that the spider "squeezed out" the first bit of line (small arrow) and the rest was then pulled out by the wind; B, Savory (1952) thought the spider produced two different lines as it descended, then broke one at the spinnerets so that it drifted free in the breeze; C, Blackwell (in McCook 1889) thought the original line was produced by moving the spinnerets apart, and additional line was then pulled out by the wind; D, Coyle (1983,1985) and Braendegaard (1938) saw spiders descend on trail lines in a strong breeze, and after the lines lengthened substantially, they broke near where they were attached.

Both Blackwall (in McCook 1889) and Nielson (1931) thought that the spinnerets are first brought together and then spread apart, thus drawing out a short span of silk, and that this short line then catches the breeze and is pulled from the spider (Fig. 1C). Recently Coyle (1983, 1985) reported field observations of the mygalomorphs *Sphodros* and *Ummidia* using their drag-lines as balloon lines; in this case the line is pulled and lengthened by the weight of the spider as it falls and is pushed by a breeze, and a free end is produced when the line breaks, apparently near the point where it was attatched to the substrate (Fig. 1D). Braendegaard (1938) had earlier made similar observations of *Dictyna borealis* O. P.-Cambridge placed in somewhat unnatural conditions (the tip of his finger).

Hingston (1920) noted that in *Argiope* " . . . the tip of the line that it gives to the wind is not a single filament but a complex structure. It is divided into a sheaf of the very finest fibrils. . . These float freely in the air and serve to support the more compact and single thread that follows them from the spinnerets." Hingston (1922) also saw that *Nephila maculata* Fabricius makes a similar set of fine lines merging to a single filament near the spider. McCook (1889) and Richter (1970) also noted multiple lines, but none of these authors clarified how these fine fibrils were originally drawn from the spider.

There are thus several contradictory and partial explanations of how airborne lines are initiated. I report here observations of at least 65 spider species, and show that different spiders use at least four different methods of initiating such lines.

## METHODS

Observations were made indoors on mature females, with a bright light and a dark background placed behind the spider so as to make lines most easily visible as they were produced. Other objects were kept at a distance so that airborne lines did not usually become tangled with them. Doors and windows were kept closed so that there was little air movement in the room. In some cases the spiders were stimulated to produce airborne lines by blowing on them gently.

Specimens of all species have been deposited in the Museum of Comparative Zoology in Cambridge, Massachusetts 02138, USA. Some specimens could not be identified to species, and are referred to by the numbers that are on labels in the vials containing the spiders.

Detailed observations of *Leucauge mariana* (Keyserling) were made using an "Emskop®" 5x magnifier mounted on a Zeiss headband magnifier, giving, in effect, a completely portable low power dissecting microscope.

## RESULTS

**Initiation using a second line.**—In some species (Table 1) spiders produced airborne lines as they descended drag-lines (Fig. 2). They attached a second line to the drag-line as they descended so that both lines were pulled from the spinnerets by the spider's weight (Fig. 2A). As the spider descended, the second line (which, judging by the amount of light it reflected, was smaller in diameter) was apparently pulled by air currents and sagged away from the straight drag-line that was sustaining the spider's weight (Fig. 2B). In some species more than one thin line emerged (footnote c in Table 1. Often the spider then stopped descending, and hung motionless while more and more thin line (up to several meters) was pulled by air currents (Fig. 2C). In some species one leg IV held the drag-line but not the thin line as the spider descended (see Eberhard 1986), but in others neither line was touched by any leg (Fig. 2). Finally, spiders often turned and climbed part way back up the drag-line before reeling in the airborne line (Fig. 2D). If the line had snagged on an object, the spider pulled it taut and attempted to walk along it to the object.

Thus, in these cases, the airborne line was initiated during descent by being drawn from the spider by gravity, and air currents then pulled it out further.

**Initiation by wrapping.**—In two species of pholcid (Table 1), the spider hung at the end of a drag-line, and pulled a line with alternate movements of its legs IV similar to those used to wrap prey (e.g. Eberhard and Briceño 1983), and the line it produced floated upward in the gentle updraft. This line may have been an extension of the drag-line, as it did not have a free end.

**"Spontaneous" Initiation.**—In some species (Table 1) the spider did not employ either of the techniques just described, but instead simply elevated its abdomen while hanging on a line or lines, or while standing on some surface (Fig. 1A),

Table 1.—Types of airborne line initiation observed. Unless noted otherwise, all spiders were mature females. Numbers and letters after genus names indicated identification numbers included in the vials housing the spiders in the Museum of Comparative Zoology. The methods of initiation refer to descriptions in the text.

| | Method of Initiation | | |
|---|---|---|---|
| Spider | Second Line | Wrap | Spontaneous |
| ARANEIDAE | | | |
| *Alpaida* TL13-6, TL31-6 | | | ? |
| *Araneus marmoreus* Clerck | + | | |
| *Azilia* TL25-1 | ?[c] | | |
| *Chrysometa* TL33-5, TL40-3, TL45-1 | + | | |
| *Cyclosa turbinata* (Walckenaer) | + | | ?[a] |
| *Enacrosomma* TL12-4, TL32-5 | + | | ? |
| *Eriophora edax* (Blackwall) | +[c,d] | | |
| *Leucauge mariana* (Keyserling) | | | + |
| *Metazygia* TL9-2,TL15-7, TL18-3,TL43-5 | + | | +?[b] |
| *Metepeira* TL45-5 | +[c] | | |
| *Micrathena fidelis* (Banks) | + | | |
| *M. gracilis* (Walckenaer) | + | | |
| *M. quadriserrata* F.O.P.Cambridge | + | | |
| *M. schreibersi* (Perty) | | | + |
| *Nephila clavipes* (Linneaus) | + | | |
| *Nephilengys cruentata* Simon | + | | |
| *Tetragnatha* TL3-2, TL9-1 | + | | |
| *Verrucosa arenata* (Walckenaer) | +[c] | | |
| *Wagneriana tauricornis* (O. P. Cambridge) | | | ? |
| THERIDIIDAE | | | |
| *Achaearanea tepidariorum* (C. L. Koch) | | | + |
| *Argyrodes caudatus* (Taczanowski) | +6 | | + |
| *Chrosiothes* | | | ? |
| *Dipoena nigra* Emerton | + | | |
| *Theridion* TL10-4, TL14-3, TL31-2 | + | | ? |
| *Tidarren* TL25-2 | + | | + |
| MIMETIDAE | | | |
| undet. genus TL60-2 | + | | |
| NESTICIDAE | | | |
| undet. genus TL10-2, TL40-3 | + | | ? |
| THERIDIOSOMATIDAE | | | |
| *Epeirotypus* FN3-7H, TL38-1 | + | | + |
| *Ogulnius* TL12-2 | | | ? |
| *Theridiosoma* TL4-2 | | | +[e] |
| *Wendilgarda galapagensis* Archer | | | +(?) |
| LINYPHIIDAE | | | |
| *Erigone* | | | ?[g] |
| "*Frontinella*" *linguatula* (F.O.P.Cambridge)TL38-3 | | | +[f] |
| *Linyphia* TL5-1 | + | | |
| undet. genus TL54-6 | + | | |
| ULOBORIDAE | | | |
| *Miagrammopes* sp., prob. *intempus* Chickering | | | ? |
| *M. simus* Chamberlin and Ivie | | | ?[h] |
| *Philoponella* sp. TL22-1 | + | | |
| *Uloborus campestratus* Simon | | | ?[h] |
| *U. glomosus* (Walckenaer) | + | | |
| *U.* sp. | + | | + |
| DICTYNIDAE | | | |
| *Dictyna* TL9-7 | + | | |
| *D.* TL44-5 | | | +[i] |

*Table 1.—Continued*

| | | | |
|---|---|---|---|
| HERSILIIDAE | | | |
| undet. genus TL44-2 | | | +[b,h] |
| SALTICIDAE | | | |
| *Beata* sp. | | | +[h] |
| *Myrmarachne* TL53-3 | + | | |
| *Paraphidippus aurantius* (Lucas) (a) | | | +[h] |
| *P. marmoratus* F.O.P.Cambridge | | | +[h] |
| *P.* sp. "ii" TL22-3, TL23-1 | +[c] | | +[h] |
| *Titanattus* TL17-1 | +(?) | | |
| undet. genus TL44-1 | + | | |
| OXYOPIDAE | | | |
| *Hemataliwa helia* (Chamberlin) | | | ?[h] |
| *H. puta* (O. P. Cambridge) | +[c] | | |
| *H.* sp. TL42-5 | +(?) | | |
| undet. genus TL55-3 | + | | |
| ANYPHAENIDAE | | | |
| *Anyphaena* | | | ?[h] |
| undet. genus TL51-1, TL14-2 | + | | |
| undet. genus TL53-2 | | | +[h] |
| CTENIDAE | | | |
| undet. genus (a) | | | ?[h] |
| AGELENIDAE | | | |
| *Agelenopsis* | +[c] | | |
| THOMISIDAE | | | |
| *Misumenops* sp. TL24-1 | +[c] | | ?[h] |
| PHOLCIDAE | | | |
| prob. *Modissimus* | | +[j] | |
| undet. genus | | + | |

[a]Initiate airborne line with very little movement along drag-line.
[b]Spider stimulated to emit airborne line when blown on.
[c]Swath of fine threads produced in addition to drag-line.
[d]Fine lines sag very little even in wind, so function as spanning or balloon line uncertain.
[e]Some with two threads in airborne line.
[f]Tip of airborne line free as spider descends.
[g]"D" form (indicative of second line method) not seen.
[h]Spread spinnerets wide as produced airborne line.
[i]Spread spinnerets, close them with a clap, and then reopen them as or just before producing airborne line.
[j]Behavior seen in field at night.

and, apparently without making any attachment of any kind, simply emitted a line. This technique appeared not to be as reliable as the others, as in some cases the spider assumed the typical posture and waited, but did not produce an airborne line. In *Leucauge mariana* such "failures" were induced by blowing gently on the spider until it assumed a typical ballooning position, then ceasing to blow.

The free ends of at least some of the spontaneously produced airborne lines were extraordinarily thin. For instance, when I observed adult *Uloborus diversus* Marx in an ideal viewing situation with very strong light from all sides and a pitch black background, I was unable to convince myself that I had found the free end of any of the many airborne lines they emitted. When I slowly reeled in the lines, the visible end moved in the gentle updraft in a way that suggested that there was an additional invisible length of line beyond the line's tip that was pulling on it. The most distal portions of airborne lines of *Leucauge mariana*

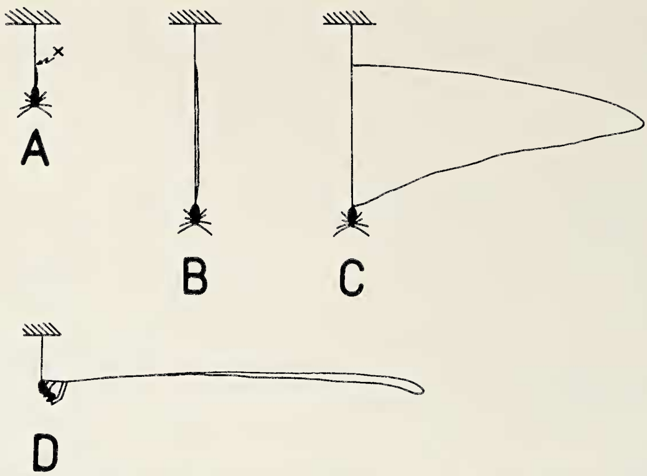


Fig. 2.—"Second line" method of airborne line initiation. A, A thin line (or swath of thin lines) is attached (at x) to the drag-line as the spider descends; B, As the spider descends further, this line is pulled from the spinnerets (along with the drag-line) by the weight of the spider's body; C, Eventually the second line becomes long enough that friction with air movements causes more line to be pulled from the spinnerets; D, Finally the spider reels in the airborne line, often having reascended the drag-line to near the point where the airborne line was initiated.

were also thin, and were not visible except when coated with talc (Fig. 3). There was usually an abrupt transition where the line suddenly became visible when these spiders produced airborne lines, presumably marking the site where thicker lines were added to or replaced thinner ones. In one case at least 20-30 cm of thin line was produced before such a transition occurred.

I was thus not able to confidently determine the exact moment of the initiation of any single airborne line. In some species, however, it was clear that the spinnerets were spread very wide (e.g. Fig. 1C) when the line was initiated (footnote h in Table 1), suggesting that the initial events were those described by Blackwall, with a short line being drawn by the movements of the spinnerets themselves, and then the pull of the breeze on this line resulting in its being drawn from the spider.

Mature *Leucauge mariana* females that were initiating airborne lines spontaneously were observed under about 7X magnification. The anterior spinnerets were held apparently immobile in their normal appressed positions before and during initiation, but the posterior lateral spinnerets were flexed to spread both laterally and posteriorly, and were occasionally clapped together and then spread again. Contrary to expectations under the Blackwell hypothesis (Fig. 1C), however, double lines were not seen emerging from these spinerets. Instead, the lines emerged from the depression between the bases of the posterior lateral spinnerets. These spinnerets were kept spread even after the emerging line had thickened and the tip was tens of centimeters away. It is possible that the line came from the short posterior median spinnerets, which were completely hidden from view. Hingston (1922) noted that the airborne line of *Nephila maculata* comes from the posterior spinnerets, but did not specify which ones.

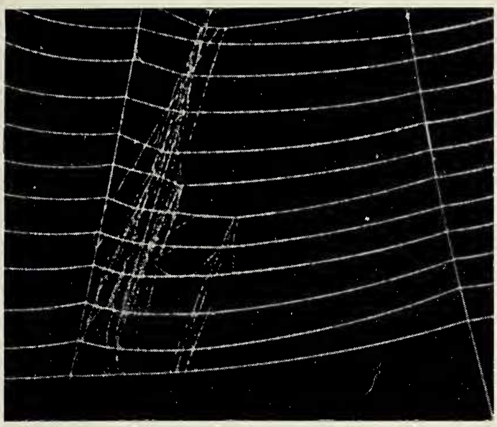

Fig. 3.—A portion of the distal portion of the multistranded airborne line produced by a mature female *Leucauge mariana*. The swath of lines was trapped on a partially completed orb web and coated with talc. Despite good viewing conditions I was not able to see this line as it emerged from the spider.

## DISCUSSION

It should be kept in mind that airborne lines have two different functions—to establish spanning lines the spider can use to walk along to reach distant objects, and to produce balloon lines that carry the spider through the air, out of contact with any other object. It is possible that different behaviors are employed to acheive these different ends. The nearly windless conditions under which my observations were made are not those in which balloon line production is elicited in some spiders (Richter 1970, Greenstone 1982). The relatively large sizes of most of the spiders I observed also suggests that the behaviors observed in this study were in general designed to establish spanning rather than balloon lines. Certainly a number of spiders did walk along their new lines when these snagged on nearby objects. The possible lack of true balloon lines may explain some differences with previous observations (e.g. the lack of the obvious differentiation of the tip of the balloon line that was noted by Hingston (1920, 1922) in *Arigiope*, and the failure to observe the apparent rupture of the drag-line seen by Richter (1970) in *Pardosa*).

Initiation of airborne lines by wrapping was seen only in pholcids, and probably represents an independent origin of airborne line production. Other related species observed under captive conditions (at least nine species of pholcids, nine species of scytodids) failed to produce any airborne lines. None of the more than 60 araneomorph species observed performed behavior similar to that reported for the mygalomorphs *Sphodros* and *Ummidia* (Coyle 1983, 1985), and the araneomorph *Dictyna* (Braendegaard 1938), but since my observations occurred under less windy conditions, it is premature to conclude that these spiders do not balloon in this manner.

The other two types of behavior are widely distributed among araneomorph spiders, and several species (uloborids, salticids, theridiids, araneids, and theridiosomatids—see Table 1) performed both types. It is possible that in those cases in which I verified that the airborne line was not attached to the drag-line (see footnote f in Table 1), it nevertheless had been attached there when it was initiated and subsequently broke free at or near the attachment. This sequence of events occurred in some but not all descents of *Micrathena gracilis* (Walckenaer) (Araneidae). This explanation requires that airborne lines break preferentially near the attachment point. Spiders apparently modulate the diameters of airborne lines (Hingston 1920, 1922, also descriptions above) as well as those of other lines (Witt et al. 1968, Wilson 1969, Work 1976), and could also possibly produce weakened attachments, so selective breakage of lines or attachments is not unreasonable. Coyle's (1983) and Braendegaard's (1938) observations of mygalomorphs and *Dictyna* suggest that selective breakage occurs in these groups.

In a number of species it seemed clear that "spontaneous" airborne line production could not have resulted from any of the other types of behavior (either the spider's spinneret area and the lines it produced were especially easy to see, or I moved objects near the drag-line and saw by the lack of tugs on the drag-line that no other lines were attached there). Thus it is clear that some species possess two alternative methods of producing airborne lines. Although other selective factors may also be involved, spontaneous initiation would be advantageous in producing given lengths of airborne line with less silk since the line is not doubled. The clear tendency for some spiders to spread their spinnerets wide as they initiated spontaneous lines accords well with Blackwell's idea that initiation involves opposite spinnerets pulling short lines from each other, but direct observations of these lines are still lacking, and Blackwell's account may have been a good guess rather than a report of actual observations. The failure to observe double lines in *Leucauge mariana* does not completely rule out the Blackwell mechanism in this species, as the original double lines might have been too thin to see. But it is puzzling that at least the thicker portion of the airborne line seemed not to emerge from the widespread posterior lateral spinnerets. No species performed the behavior described by Savory (1952—see Fig. 1B), and it seems likely that he actually observed the second line method (Fig. 2) but failed to notice the bottom portion of the airborne line.

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